HUMMINGBIRD LICKING BEHAVIOR AND THE ENERGETICS OF NECTAR FEEDING

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ABSTRACT.—Key assumptions and components of biophysical models of hummingbird licking that are central to current interpretations of plant-pollinator coevolution have not previously been verified. To test the realism of the models, I measured fine-scale parameters of a Rufous Hummingbird's (*Selasphorus rufus*) licking, including licking frequency and volume extracted per lick, with a photodetector array that monitored movement of the tongue and the nectar-pool meniscus. Both licking frequency and volume per lick decreased with increasing concentration, contradicting previous suggestions that hummingbirds may maintain constant licking frequency or volume per lick at all concentrations. At three nectar-pool volumes, energy-intake rates were significantly higher at 25 to 35% sucrose than at higher concentrations, supporting the models' qualitative prediction that optimal nectar concentration is low when energy-intake rate is averaged over the time scale of licking. *Received 21 October 1993, accepted 1 April 1994.*

THE ADAPTIVE SIGNIFICANCE of low nectar concentrations prevalent in hummingbird-pollinated flowers has attracted much attention (Baker 1975, Bolten and Feinsinger 1978, Calder 1979, Pyke and Waser 1981, Plowright 1987). Mean nectar concentrations of North American and many tropical hummingbird-pollinated plants average 20 to 25% sucrose equivalents (mass/total mass; Baker 1975, Pyke and Waser 1981, Heyneman 1983). In choice tests, however, hummingbirds have preferred concentrations higher than 45% (Van Riper 1958, Hainsworth and Wolf 1976, Stiles 1976, Pyke and Waser 1981, Tamm and Gass 1986). This preference for concentrations roughly twice what flowers offer in nature has complicated understanding of the presumably coevolved plant-pollinator system (Pyke and Waser 1981, Feinsinger 1987, Gass 1988).

Optimal nectar concentration for hummingbirds should be predictable from the details of their feeding behavior and fluid-dynamical properties of nectar. Hummingbirds feed by licking with their forked, open-grooved tongues, into which nectar flows by capillary action during the loading phase when the tongue contacts the nectar pool (Weymouth et al. 1964, Hainsworth 1973, Ewald and Williams

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1982). Increasing concentration increases the nectar's caloric value, but also increases its viscosity and, therefore, decreases its volumetric-flow rate into the tongue grooves. The combination of these effects causes energy-intake rate to peak at an intermediate concentration (Heyneman 1983, Kingsolver and Daniel 1983). Biophysical models (Kingsolver and Daniel 1983) suggested that the sucrose concentration that maximizes birds' energy-intake rates is 20 to 25% for low nectar-pool volumes that can be loaded on single licks, but 35 to 40% for high volumes that require many licks to empty.

The model prediction that optimal concentration depends on nectar-pool volume seemed to resolve the discrepancy between birds' observed preference for high nectar concentrations and the low concentrations many flowers provide them. All published choice tests used feeders containing volumes that were essentially infinite from the birds' perspective, and for which the model predicted high optimal concentration. In contrast, most flowers visited by nontraplining hummingbirds usually contain nectar pools near to or less than the volume of the tongue grooves (which is 1.9 μl for Rufous Hummingbirds [*Selasphorus rufus*]; unpubl. data; pool volumes for several plant species are summarized in Gass and Roberts 1992). Under these conditions, when the nectar pool could be emptied on a single lick, the model predicted low optimal concentration.

The predicted upward shift in optimal con-

centration with increasing volume does not, however, result from increasing volume per se (Gass and Roberts 1992). Instead, it is a consequence of increasing the time scale of integration of the intake-rate equations from the duration of tongue loading during a single lick to the complete licking cycle, which includes the duration of the unloading phase required to transfer nectar from the tongue into the bird's bill. Accordingly, hummingbirds should prefer dilute nectar only if they maximize energy-intake rates at the very fine time scale of the loading phase of single licks alone, but should prefer higher concentrations even at very low nectar volumes if they maximize over the licking cycle, over total handling time at flowers, or over some coarser time scale.

Testing the models that predict optimal nectar-sugar concentrations has been hampered by hummingbirds' high licking frequency, and by the fact that their bills and tongues are small, as are the nectar pools and the flowers that they visit (Ewald and Williams 1982, Paton and Collins 1989). Only two previous studies have estimated parameters of the hummingbird licking cycle, using cinematography to investigate licking from high-volume feeders (Hainsworth 1973, Ewald and Williams 1982). Hainsworth (1973) probably used a camera with too slow a speed to capture all licks during feeding (Ewald and Williams 1982). Ewald and Williams (1982) used a higher camera speed, but licking was not filmed at a range of concentrations.

Without reliable measures of licking parameters at a range of concentrations and nectar volumes, models have had to incorporate assumptions about them. Two possible behaviors that hummingbirds might exhibit were proposed by Kingsolver and Daniel (1983; see also Gass and Roberts 1992). The tongue might load a constant volume at all concentrations (constant-volume licking). In this case, if concentration increases, loading time must increase and licking frequency decrease. Alternatively, licking frequency could be constant at all concentrations (constant-frequency licking), in which case if concentration increases, the volume loaded per lick must decrease.

There is no evidence for either of these proposed licking behaviors or any others; my study was designed to help meet this need. I used an electronic photodetector apparatus to measure parameters of hummingbird licking and to estimate energy-intake rates at the time scale of

the licking cycle, for a range of concentrations and volumes.

METHODS

I tested one adult male Rufous Hummingbird between 3 August and 14 September 1991. This individual was captured at Rosewall Creek on Vancouver Island in May 1991. Its bill length was 16.6 mm from the tip to the base of the exposed culmen, and its mass ranged from 3.3 to 4.7 g over the course of these tests. Although variations in body mass probably influenced the bird's overall energy requirements and its hovering cost while feeding, I observed no effects on the details of its licking behavior. When not in tests, the bird had free access to a commercial hummingbird food, Nektar Plus (Nekton USA, Inc.) supplemented with soybean protein. During these experiments, the bird was housed in a Plexiglas box (46 cm long × 29 cm wide × 43 cm high).

Parameters of licking behavior were measured with a photodetector array. The array was a linear series of four infrared emitters facing a parallel series of four detectors (Motorola pin-diode components MLED71 and MRD721, respectively) on opposite sides of a glass feeder tube. The tube was closed at the far end, with internal dimensions of 1 mm square by 16 mm deep. This depth was within but near the limit of tongue extension for a male Rufous Hummingbird of this size (Temeles and Roberts 1993). The tube was inserted into the array such that each emitter's light passed horizontally across it to the matching detector on the other side. The centers of the light beams were 4.65 mm apart, and were 1.55, 6.20, 10.85 and 15.50 mm from the feeder tube opening (distances ± 0.05 mm). The cross-sectional radius of each light beam was 0.86 mm.

During each lick, the hummingbird's tongue interrupted each light beam in sequence, and the resulting voltage reductions were monitored with a Nicolet 4094/4851 four-channel digital oscilloscope. Breaking the light beam of the first emitter-detector unit triggered data recording from all four channels of the oscilloscope. The feeder tube admitted only the bird's tongue, so measurements encompassed only the licking cycle and excluded the time required to position and insert the bill (Gass and Roberts 1992).

Nectar was dispensed into the far end of the feeder tube from the opening, so the bird's tongue had to travel farther to contact the nectar pool at low than at high volumes. The cross-sectional area of the tube was 1 mm², so 1 μl of solution filled 1 mm of its length.

To begin each trial, I inserted the loaded feeder tube into the array and uncovered the feeder, allowing the bird to feed. On several trials, the bird briefly paused while feeding, probing the feeder more than once. In addition, it did not always empty the feeder. Both of these cases occurred more often when both nectar-pool volume and concentration were high. I

analyzed only trials on which the bird fed without pausing and removed all the nectar provided during a single probe of the feeder (45% of all trials). After every trial I covered the photodetector array, then removed and visually inspected the feeder tube to determine if the bird had emptied it. With a repeating dispenser, I then refilled the feeder tube for the next trial. For each combination of concentration and volume, trials were continued until four uninterrupted feeding visits had been recorded. Testing sessions lasted 45 min to 5 h, and were held no more than once each day.

The hummingbird was tested at 20 combinations of sucrose concentration and nectar-pool volume: 25, 35, 45 and 55% at 1, 4, 8, 12 and 16 μl ($\pm$0.02 μl). Although I also offered 65% sucrose, the bird never emptied the feeder during a single visit at this concentration. The bird also failed to empty the 55% solution when only 1 μl was provided.

Using this protocol, I measured the number of licks and the time ($\pm$1 ms) the bird took to remove food from the feeder. For each trial I calculated average licking frequency (number of licks/extraction time), average lick volume (nectar volume/number of licks), and average volume-intake rate (nectar volume/extraction time) during licking. I also calculated average energy-intake rate (E) in watts during licking with the following equation:

$$E = \epsilon Sv\rho/t, \qquad (1)$$

where ϵ is the energy content of sucrose (0.01648 J/μg), S is the sucrose concentration (%), v is the nectar volume (μl), t is time (s), and ρ is the density of sucrose solution (μg/μl), obtained by fitting a curve to tabulated values (Weast 1977),

$$\rho = 1.8(10^{-5})S^2 + 3.725(10^{-3})S + 0.999 \qquad (2)$$

(corrected $r^2 > 0.99$).

Because sucrose solution has a different refractive index than air, nectar and air registered differently on the oscilloscope traces. This allowed me to time the recession of the nectar pool meniscus past the four light beams during licking on the 16-μl trials, when the nectar pool completely filled the feeder tube. Therefore, I was able to estimate changes in volume and energy-intake rates within individual visits as the bird emptied the feeder. It was not possible, however, to measure precisely the distance the tongue was extended or the volume loaded on each individual lick, nor to measure the durations of the loading and unloading phases of the licking cycle.

To examine the significance of the effect of concentration on energy-intake rate during licking, I performed a Kruskal-Wallis test for each nectar-pool volume, using the NPAR procedure in SYSTAT. When a significant effect was detected for a nectar-pool volume, I performed a nonparametric Tukey-type multiple-comparison test (Zar 1984) for all pairs of concentrations at that volume.

RESULTS

Hummingbird nectar feeding was more complex than previously modelled. The rate of nectar extraction was not constant within visits; both lick volume and volume-intake rate were low initially, increased briefly, and then decreased as the hummingbird emptied the feeder (Figs. 1A and 1B). This effect was most striking at 55% sucrose. Licking frequency, however, was relatively constant within visits at a given concentration (Fig. 1C).

The hummingbird exhibited neither the constant-frequency nor the constant-volume licking behaviors previously envisaged. As sucrose concentration increased, lick volume did not decrease enough to keep licking frequency constant, nor did licking frequency slow enough to keep lick volume constant. For all nectar-pool volumes provided, both average licking frequency and the average volume the bird loaded per lick decreased with increasing concentration (Figs. 2A and 2B).

Average lick volume, volume-intake rate, and energy-intake rate during licking were higher at higher nectar-pool volumes, in which the tongue could be immersed more deeply. Across the concentrations presented, the bird gained energy more than four times as rapidly at 16 μl than at 1 μl (Fig. 2D).

Kruskal-Wallis analyses of variance indicated significant differences in energy-intake rate with concentration for the 1-, 12- and 16-μl trials (Table 1). At each of these three nectar-pool volumes, nonparametric Tukey-type multiple comparison tests revealed significant differences between the two concentrations in the range offered that yielded the highest and lowest energy-intake rates. At 1 μl, the rate was higher at 35% than at 25% ($P < 0.05$); at 12 μl, the rate was higher at 25% than at 55% ($P < 0.025$); and at 16 μl, the rate was higher at 35% than at 55% ($P < 0.025$).

DISCUSSION

Hummingbirds exhibit considerable interspecific variation in foraging behavior and in bill and tongue morphology, so my results for a Rufous Hummingbird may not be representative for all species. For example, my finding of decreased licking frequency with increasing concentration is the opposite of the pattern found by Hainsworth (1973) for Black-chinned
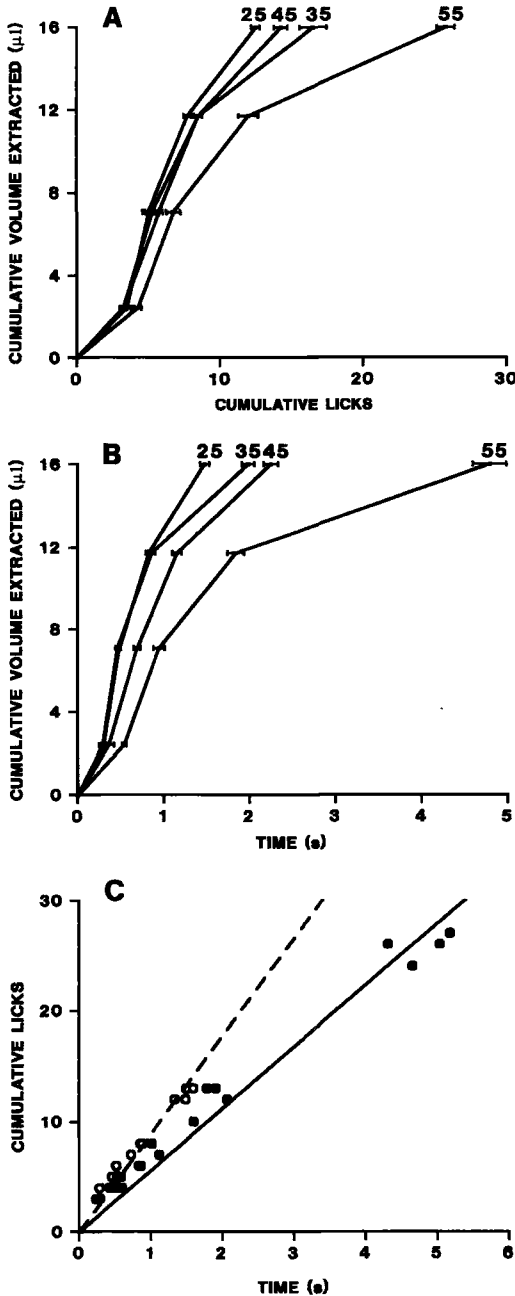
TABLE 1. Kruskal-Wallis analysis of variance of energy-intake rate during licking cycle with concentration.

Volume (μl)	H	df	n	P
1	6.500	2	12	0.039
4	2.140	3	16	0.544
8	5.316	3	16	0.150
12	9.419	3	16	0.024
16	8.404	3	16	0.038

(*Archilochus alexandri*) and Blue-throated hummingbirds (*Lampornis clemenciae*). That pattern, however, is likely spurious because of the low camera speed used (Ewald and Williams 1982, Gass and Roberts 1992). Nevertheless, the lowest licking frequencies I measured (4.9 to 5.9 Hz at 55% sucrose on 16-μl trials) were near the value of 4.7 Hz reported for Blue-throated Hummingbirds feeding at the same concentration (Hainsworth 1973). If species other than Rufous Hummingbirds also lick more slowly at higher concentration, film records in the earlier study would have captured a larger proportion of all licks at high than at low concentration. Therefore, Hainsworth's (1973) measurements at 55% sucrose may be accurate, even though his values for low concentration probably are not.

The values I recorded for licking performance were lower than those of Anna's Hummingbirds (*Calypte anna*) reported by Ewald and Williams (1982). The highest average licking frequencies I measured (at 25% sucrose during 12-μl trials), were 9.1 to 9.7 Hz, whereas the mean for Anna's Hummingbirds feeding on approximately 22% sucrose was 13.8 Hz (Ewald and Williams 1982). The highest lick volumes and volume-intake rates during licking I measured were 0.9 to 1.2 μl/lick and 7.3 to 10.4 μl/s, respectively (both at 25% during 16-μl trials), as compared to 1.2 μl/lick and 17 μl/s for Anna's Hummingbirds (Ewald and Williams 1982). These differences may be due to Anna's Hummingbirds having a larger tongue-groove volume (ca. 2.8 μl; Ewald and Williams 1982). Alternatively (or additionally), the differences may relate to feeder design; unlike mine, the feeder

Fig. 1. Variation in licking performance within single visits. Lines in A and B connect means of four 16-μl trials for four sucrose concentrations (%). Because volume measurements were taken at four fixed points along photodetector array, variation in A and B is in number of licks and time; error bars indicate SE. Lines in panel C are least-squares regressions, constrained to intercept the origin, on data for four 16-μl trials at 25% (hollow circles, dashed line; R^2 = 0.990) and 55% sucrose (solid circles, solid line; R^2 =

←

0.986). Slopes of lines describe (A) lick volume, (B) volume-intake rate, and (C) licking frequency.
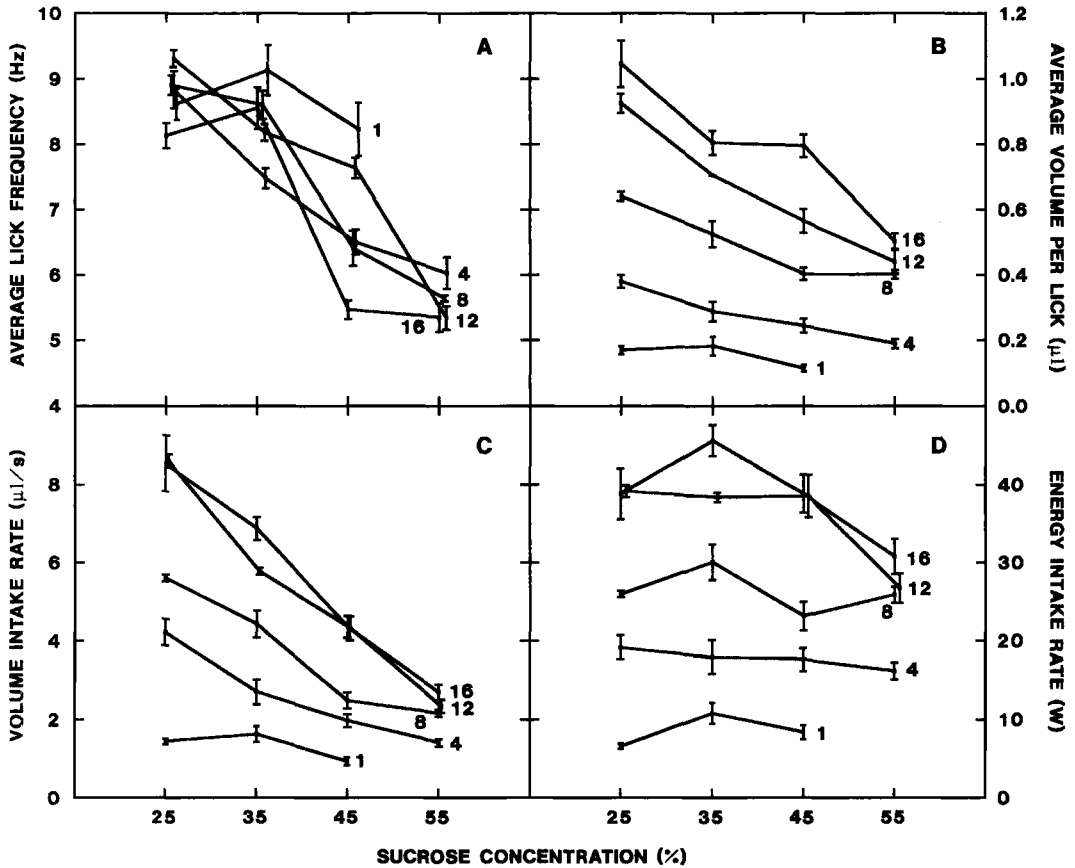
Fig. 2. Variation in parameters of licking behavior with sucrose concentration, averaged over visits. Lines connect means of four trials at each concentration for four nectar-pool volumes (μl). Error bars indicate SE. Wherever means overlap at different nectar-pool volumes, plots for each volume are staggered along X-axis to allow them to be distinguished.

used by Ewald and Williams (1982) did not exclude birds' bills or surround tongues closely, so licking could have been easier for the birds in their study. Because feeder design influences the quantitative results of foraging ability studies (Grant and Temeles 1992), application of these measurements to other situations should be undertaken with caution. In addition, few flowers normally visited by short-billed species like Rufous Hummingbirds have corollas that are both long and narrow like my feeder tube, excluding the bill and requiring long tongue extension (Feinsinger pers. comm.).

The reason why lick volume and volume-intake rate were both low at the beginning of a feeder visit is unclear (Figs. 1A and 1B). This low initial performance may have been due to exploratory probing, during which the hummingbird made adjustments to its position to

lick more efficiently. Exploratory licking apparently is reduced when flower corollas are shaped to guide birds' bills and tongues to the nectar pool, resulting in increased licking success (Ewald pers. comm.). Consequently, the low initial licking performance I observed may be an artifact of my feeder design.

Previous workers have suggested that deep immersion should free tongue loading from the constraints of capillarity-induced nectar flow, yielding higher optimal concentrations at high volumes (and deeper immersion) than at low volumes for which only the tongue tip can contact the nectar pool (Hainsworth 1973, Kingsolver and Daniel 1983). Contrary to this prediction, I found that energy-intake rates did not appear to be maximized at higher concentrations when nectar-pool volumes were higher (Fig. 2D). Apparently, the increased viscosity of

high concentrations limits loading rate even when nectar can enter the tongue grooves along their length. In nature, however, Rufous Hummingbirds would be unlikely to encounter flowers that provide both high nectar-pool volumes and concentrations, as these are pollinated almost exclusively by hermits and long-billed trochiline hummingbirds (Feinsinger and Colwell 1978, Feinsinger pers. comm.).

Earlier studies' measurements at the coarser time scale of feeder visits (adding bill-insertion and retraction time to licking cycle) have shown that intake rates increase with increasing nectar-pool volume (Montgomerie 1984); my results are similar. These findings are consistent with Gass and Roberts' (1992) conclusion that intake rates during the licking cycle are higher at high-volume feeders than at flowers. The fact that in my experiment the average licking frequency did not vary consistently with nectar-pool volume (Fig. 2A), and was relatively constant even as the nectar pool receded during licking (Fig. 1C), indicates that variation in average lick volume is principally responsible for variation in volume and energy-intake rates with nectar-pool volume.

Because average lick volume is lower when nectar pools are small (Fig. 2B), one would predict that lick volume should decrease with successive licks during a single visit to a flower, as the nectar pool is depleted and tongue immersion decreases (Gass and Roberts 1992). My measurements supported this prediction (Fig. 1A).

The observed decrease in average volume-intake rate over the licking cycle with increasing concentration (Fig. 2C) corroborates results of earlier studies at coarser time scales (Montgomerie 1984, Tamm and Gass 1986), and follows predictions of biophysical models of nectar feeding (Heyneman 1983, Kingsolver and Daniel 1983). My finding that licking frequency decreases with increasing concentration indicates that hummingbirds can partly conserve loading time and therefore lick volume, thus achieving higher volume-intake rates during licking than if licking frequency remained constant (Gass and Roberts 1992).

The hummingbird in my experiment never completely emptied 65% solutions from the feeder, and did not empty 55% solutions when only 1 μl was offered. These solutions were probably too viscous for the bird to extract easily from the end of the 16-mm-long feeder tube, near the limit of its tongue extension (Temeles

and Roberts 1993). Within feeding visits, the volume-intake rate during licking decreased more dramatically at high than at low concentration as the nectar pool receded (Fig. 1B). This observation leads to the suggestion that hummingbirds may prefer low concentrations in flowers with very long corollas, where the time and energy costs of harvesting nectar would be high. Consequently, concentration preference may depend on corolla length. Furthermore, given that tongues of female hummingbirds are longer than those of males (Johnsgard 1983, Paton and Collins 1989, Temeles and Roberts 1993), females' feeding performance may be less constrained by corolla length (Grant and Temeles 1992, Temeles and Roberts 1993). Females, therefore, may prefer higher concentrations than males under identical conditions.

Most flowers are wide enough to allow bill insertion, and species with long corollas are visited mainly by long-billed hummingbirds, so dependence of Rufous Hummingbirds' concentration preference on corolla length may not be observed in nature. Interestingly, however, flowers in the Acanthaceae that are pollinated by long-billed hummingbirds have longer and narrower corollas, and offer lower sugar concentrations than usually found in flowers pollinated by these birds (Feinsinger pers. comm.).

My experiment provides a basis for distinguishing between time scales at which Rufous Hummingbirds' concentration preferences maximize their energy-intake rates. For 12- and 16-μl nectar pools, 25 to 35% sucrose yielded significantly higher energy-intake rates over the licking cycle than did 55%. This is probably true for smaller nectar pools as well, given that the bird failed to extract the 55% solution when 1 μl was presented. Therefore, if birds maximize energy-intake rates over the duration of licking, they should be expected to prefer 25 to 35% concentrations over 55% or higher concentrations. In all high-volume choice tests, hummingbirds have preferred concentrations higher than 25 to 35% sucrose (Van Riper 1958, Hainsworth and Wolf 1976, Stiles 1976, Pyke and Waser 1981, Tamm and Gass 1986). This means that at large nectar pools, decisions by birds maximize their energy-intake rates at some time scale coarser than the licking cycle.

However, a possibility exists that, when the nectar pool is small enough to be loaded on a single lick, birds average the energetic costs and benefits of feeding over only the loading phase

of single licks, and would prefer low concentrations. It is probably unrealistic, though, to imagine that hummingbirds would lick only once even at nectar pools much smaller than tongue-groove volume. In this study, five or more licks were taken when 1 μl was provided. More than a single lick may be required to convince a bird that a flower or feeder is empty and, because they can lick so rapidly, the time cost of double-checking is small. If birds lick more than once at all volumes, they would be expected to choose the same concentrations at all volumes. Clearly, low-volume choice tests are required to address this issue.

Although hummingbird preference tests are relevant to coevolutionary theories about patterns of nectar concentration in nature, interpretation should be undertaken with caution, because plant fitness is affected not only by pollinator visitation, but also by the amount of energy invested in nectar rewards (Pyke and Waser 1981). Furthermore, focussing on patterns of average concentrations in hummingbird-pollinated flowers obscures considerable variation (Kingsolver and Daniel 1983). For example, nectars of 17 species in Arizona and Colorado ranged from 8 to 43% sucrose equivalents (Hainsworth 1973). Even within individual flowers, concentration varies greatly after secretion with environmental factors, particularly ambient humidity (Plowright 1981, Bertsch 1983). The persistence of such wide variation may argue against nectar concentration per se being subject to strong selection pressure from hummingbirds.

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